Current Biology 24, 2935–2939, December 15, 2014 ©2014 The Authors http://dx.doi.org/10.1016/j.cub.2014.10.036

Report

Conflict between Groups Promotes Later Defense of a Critical Resource in a Cooperatively Breeding Bird

Andrew N. Radford[1,*] and Tim W. Fawcett[1]

[1]School of Biological Sciences, University of Bristol, 24 Tyndall Avenue, Bristol BS8 1TQ, UK

Summary

Conflict between groups (intergroup conflict) is common in many social species [1–4] and is widely discussed as an evolutionary driver of within-group dynamics and social structure [2, 5]. However, empirical studies investigating the impacts of intergroup conflict have focused on the immediate aftermath [6–9], when behavioral changes may be the direct result of elevated stress levels [7] or territorial exclusions [9]. Demonstrations of longer-term effects, with behavioral changes persisting once increases in stress have diminished and full access to resources is again possible, would support proposed links to individual fitness and social evolution. Here we show that conflicts between neighboring groups of cooperatively breeding green woodhoopoes (*Phoeniculus purpureus*) have a lasting influence on decisions concerning roost cavities, a limiting resource vital for survival and breeding. Groups involved in extended conflicts in the morning were more likely to return to the zone of conflict that evening, roosting closer to territorial borders, than when intergroup interactions were short or did not occur. Extended morning conflicts also increased the likelihood that groupmates roosted together and preened one another at the roost, suggesting that intergroup conflict promotes consensus decision-making, social bonding, and group cohesion. Border roost use and allopreening increased more following conflicts that were lost rather than won. By demonstrating that both the intensity and outcome of intergroup interactions affect resource defense and associated within-group behavior many hours later, our results begin to bridge the gap between the immediate impacts of intergroup conflict and its role in social evolution.

Results

Green woodhoopoes (*Phoeniculus purpureus*) live in groups consisting of a dominant breeding pair and up to six nonbreeding helpers of both sexes [10]. Each group defends a year-round territory (mean ± SE area = 23.5 ± 1.7 hectares) in thickly forested valleys [11], and they generally forage and move around this territory as a single unit [12]. Group members roost communally in tree cavities every night, which yields vital thermoregulatory benefits [13], and use one of the same cavities for nesting [10]. Each territory contains only a small number (mean ± SE = 6.9 ± 2.9) of suitable tree cavities [10], and these represent the limiting resource for woodhoopoe survival and reproduction: groups will move rapidly into previously unoccupied areas of forest if nest boxes are provided [14].

Interactions between groups are common and involve all group members contributing to alternating choruses (or "rallies") [1], which on rare occasions escalate to physical fighting [15]. Around 97% of intergroup interactions (IGIs) between neighbors take place within 100 m of shared territory boundaries, termed zones of conflict [16]. We found that cavities in zones of conflict were used for roosting significantly more often than would be expected by chance (Wilcoxon signed-ranks test: $Z = 2.05$, $n = 12$, $p = 0.041$; Figure 1A). Groups with a greater involvement in IGIs, compared to those that interacted less with their neighbors, used zone-of-conflict roosts relatively more often than predicted from their availability (Spearman rank correlation, IGI rate: $r_s = 0.59$, $n = 12$, $p = 0.042$; proportion of time engaged in IGIs: $r_s = 0.62$, $n = 12$, $p = 0.032$; Figure 1B).

Woodhoopoe IGIs are highly variable in duration (1–45 min) and exhibit a bimodal distribution: "short" IGIs (>57% of cases), usually on territory boundaries, are decided within 5 min and primarily involve information exchange about current group structure and potential breeding opportunities, while "extended" IGIs (~30% of cases), which develop when there is a conflict over territory space, take >15 min to resolve and usually involve a territorial intrusion [15]. We found that self-preening, a potential indicator of stress levels in this species [16, 17], was not significantly affected by the occurrence of short IGIs (linear mixed model [LMM] using mean duration of self-preening bouts: $\chi^2_2 = 0.23$, $n = 44$, $p = 0.900$), but there was a highly significant effect of extended IGIs ($\chi^2_2 = 11.40$, $n = 42$, $p = 0.003$). Specifically, self-preening bouts lasted significantly longer in the immediate aftermath of an extended IGI than in the period immediately preceding the conflict (Figure 2). The fact that self-preening was unaffected by short IGIs, and the fact that no diurnal fluctuations in self-preening were evident on days without IGIs (A.N.R., unpublished data), strongly suggests that the increase immediately following an extended IGI is a direct response to intense conflict. However, this effect was short lived: by the start of the afternoon observation session, long before groups roosted (mean ± SE time from start of observation session to roosting = 3.5 ± 0.2 hr, range = 2.2–4.5 hr, $n = 16$ days), the duration of self-preening bouts had returned to pre-IGI levels (Figure 2).

Despite no evidence of prolonged stress, and despite groups always (100% of 134 cases) moving away from the IGI site in the interim, the occurrence and type of IGIs in the morning (none, short IGI, extended IGI) significantly influenced the likelihood of roosting within a zone of conflict at the end of the day (generalized linear mixed model [GLMM]: $\chi^2_2 = 23.30$, $n = 232$, $p < 0.001$). Specifically, zone-of-conflict roosts were more likely to be chosen on evenings when there had been an extended IGI that morning compared to on evenings when there had been a short IGI or no IGI that morning (Figure 3A). Even when controlling for whether a group had roosted in the zone of conflict the night before (by including the location of the previous night's roost for the subset of observations for which this information was known), the effect of IGI categorization remained highly significant ($\chi^2_2 = 13.88$, $n = 153$, $p = 0.001$). Further analysis showed that the effect of IGI categorization was not because groups were more likely

*Correspondence: andy.radford@bristol.ac.uk

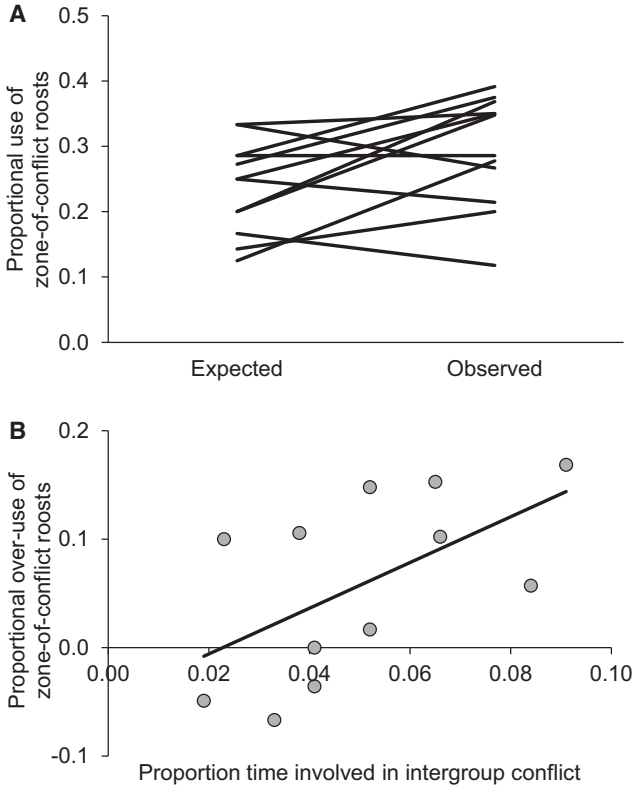

Figure 1. Relative Use of Roosts in a Zone of Conflict

(A) Expected (relative to total number of roosts available in the territory) and observed proportions of zone-of-conflict roosts used.

(B) The difference between observed and expected usage of zone-of-conflict roosts in relation to the proportion of observation time engaged in intergroup conflict; the least-squares regression line is shown. n = 12 groups.

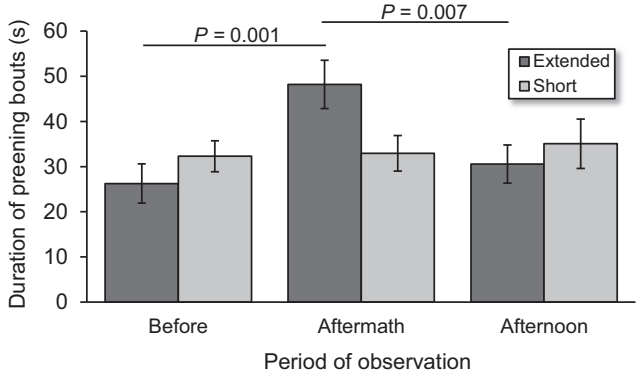

Figure 2. The Influence of Intergroup Interactions on Self-Preening Bouts

The effect of extended and short intergroup interactions (IGIs) on the duration of self-preening bouts in the 30 min immediately before the IGI ("before"), immediately after the IGI ("aftermath"), and at the start of the afternoon observation session 7.7 ± 1.1 hr (mean ± SE) later ("afternoon"). Means ± SE are shown, along with p values for significant post hoc comparisons. n = 8 (extended IGIs) and n = 10 (short IGIs) groups.

to change roost sites on extended IGI days ($\chi^2_2 = 4.44$, n = 153, p = 0.109), but because groups that changed roost were more likely to move to a roost closer to the shared border on nights following an extended IGI than on nights when there had been a short IGI or no IGIs that morning ($\chi^2_2 = 9.52$, n = 64, p = 0.009; Figure 3B).

When groups roosted within a zone of conflict, their time of arrival at the roost site was significantly affected by IGI categorization (LMM: $\chi^2_2 = 6.68$, n = 70, p = 0.035): they arrived earlier on days when they had experienced an extended IGI than on other occasions (Figure 4A). There was, however, no significant difference in the time they entered the roost for the night depending on IGI categorization ($\chi^2_2 = 0.13$, n = 70, p = 0.938). On most nights, all groupmates roosted together in a single cavity, but occasionally groups split up more than 20 min before roosting and spent the night in two different cavities, as found previously in this species [18]. There was a strong but marginally nonsignificant tendency for groups to split less often on days when there had been an extended IGI (GLMM: $\chi^2_2 = 5.95$, n = 70, p = 0.051; Figure 4B).

Allopreening between woodhoopoe groupmates (an established affiliative behavior [19]) has previously been shown to change in the hour following an IGI, with dominant individuals increasing their preening of subordinates [7, 20]. In the current study, we found that the likelihood of groups exhibiting allopreening in the evening when roosting in the zone of conflict was significantly influenced by IGI categorization that morning (GLMM: $\chi^2_2 = 8.27$, n = 70, p = 0.016): allopreening was more likely on extended IGI days than in other cases (Figure 4C).

Extended IGIs usually have clear-cut winners and losers; neighboring groups that intrude and win extended IGIs spend up to an hour in the territory of their opponent, foraging and examining tree cavities [15]. We therefore considered whether roost choice in the evening is affected by the outcome of earlier intergroup conflicts, testing the prediction that there is a stronger response following lost encounters, as is the case with intragroup behavior in the immediate aftermath of IGIs [7]. Considering only days when there was an occurrence of an extended IGI in the morning, there was a strong though nonsignificant trend for groups to be more likely to roost in the zone of conflict when they had lost rather than won the conflict (GLMM: $\chi^2_1 = 2.90$, n = 54, p = 0.089; Figure 3C). There was no significant difference in arrival time depending on conflict outcome (LMM: $\chi^2_1 = 0.81$, n = 31, p = 0.368), but groups were significantly more likely to exhibit allopreening before roosting when they had lost rather than won the morning conflict (GLMM: $\chi^2_1 = 3.98$, n = 31, p = 0.046; Figure 4D).

Discussion

Our findings provide strong evidence that intergroup conflict can influence group decisions and intragroup behavior relating to critical resource use. In general, green woodhoopoe groups that interacted more with their neighbors used roosts near territorial borders more often. Use of border roosts was most pronounced when there had been an extended IGI earlier in the day, especially if that conflict had been lost. Extended IGIs in the morning were also associated with a greater likelihood of group members roosting together in one place and allopreening at the roost site in the evening, suggesting that conflict with rivals promotes consensus over roosting decisions and group cohesion. Our results indicate that subsequent behavior is influenced by both the nature of the interaction with another group (extended but not short IGIs, in this case) and the outcome of a conflict (see also [7, 9, 20]). Most importantly, we demonstrate that the behavioral impact of intergroup conflict is longer lasting than the immediate effect considered in many previous studies ([7, 8, 21],

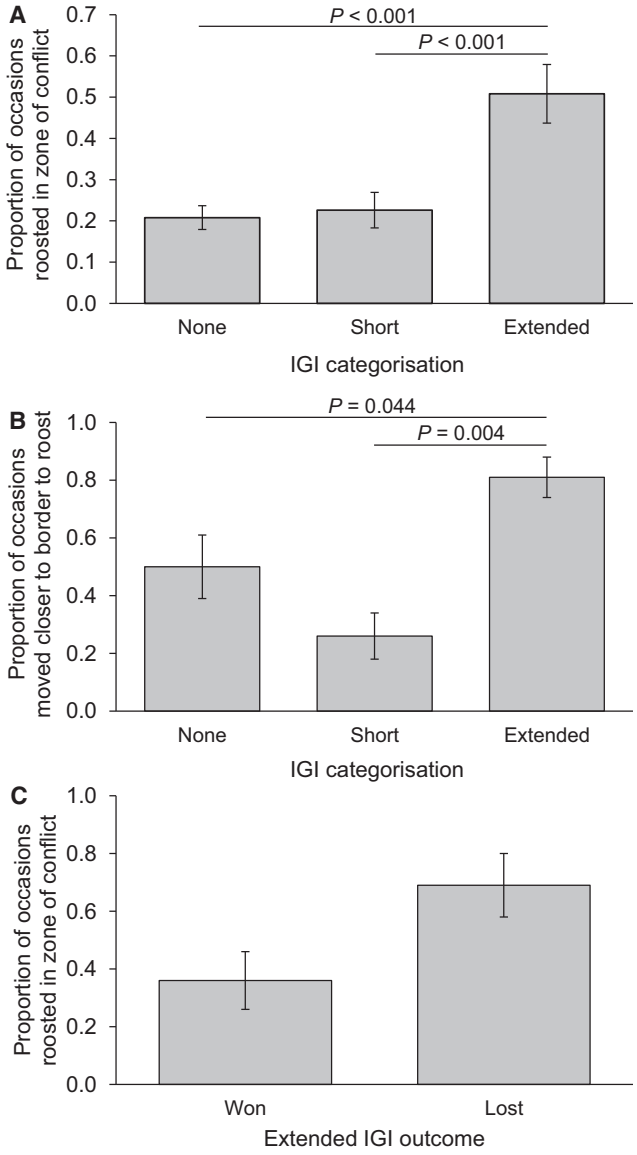

Figure 3. The Influence of Intergroup Interactions on Roost Use

(A and B) The effect of IGI categorization (extended, short, or no IGI in the morning) on the proportion of occasions in which a zone-of-conflict roost was used that evening (A) and in which the group chose a roost closer to the relevant territorial border that evening as compared to the night before (B).

(C) The effect of extended IGI outcome on the proportion of occasions in which a zone-of-conflict roost was used that evening.

All panels show means ± SE, with p values for significant post hoc comparisons. n = 12 groups.

but see [9, 22]) and can occur without territorial exclusions (cf. [9, 22, 23]) and once elevated stress levels have subsided.

Previous work on intergroup conflict has shown that losing groups might be prevented from using certain areas because of exclusion by winners [9, 23] or may avoid areas of agonistic interaction if prior experience reliably predicts future conflict [22]. This reduced involvement in agonistic interactions parallels the "loser effect" often found in dyadic contests, whereby individuals become less likely to escalate future conflicts following a defeat (reviewed in [24]). Even where loser effects are not found, previous fights can reduce aggression and discourage home-range overlap [25, 26]. Here, however, we found the opposite effect: the woodhoopoe groups in our study used roosts in zones of conflict *more* often following intergroup conflicts, especially conflicts that were lost, and arrived at roost sites earlier on such occasions. This greater usage may represent defense of a limiting resource; as in many other species [23, 27, 28], there is a risk that highly productive or important parts of a territory will be annexed by successful rival groups [29]. Despite this risk, groups may continue to use other roosts outside the zone of conflict if they provide greater thermoregulatory benefits [13], provide more protection from predators [29], or are less likely to accumulate water on rainy nights [30], or if switching roosts is important for minimizing the buildup of parasites [31].

Occasions when members of the same group roost in different places probably reflect unresolved between-individual conflicts of interest over group decisions [32, 33]. Our results suggest that an earlier conflict with a rival group enhances the likelihood that a consensus will be reached later on, i.e., that all group members roost together. Since all adult woodhoopoe group members contribute to the majority of IGIs [1] and the outcome of extended IGIs is strongly determined by relative group size [15], an increased need for collective defense may override within-group disagreements about roost site. Previous work on the factors influencing group fissions has focused on environmental variability and uncertainty, as well as within-group factors such as individual energetic state, the social relationships between group members, and the ways in which information is gathered and shared [34–36]. Our study suggests that external factors—in this case, intergroup conflict—also play an important role and should be considered in future work on consensus decision-making.

Extended intergroup conflicts appear to cause short-term increases in stress, which may be responsible for previously documented changes in allopreening and other behavior in the immediate aftermath [7, 37]. However, our data on self-preening suggest that those increased stress levels subside long before groups arrive at the roost site, perhaps because commonly exhibited postconflict affiliative behavior between groupmates reduces stress for both recipients [38, 39] and donors [17, 40]. Consequently, the greater allopreening at roost sites on days when there had been an extended IGI in the morning is unlikely to be explained by lingering stress from the earlier conflict. One alternative possibility is that returning to the zone of conflict in the evening causes a secondary stress increase, especially since conflicts reliably occur in the same areas. Previous work has indicated that merely being in a zone of conflict can affect intragroup behavior [16], but here we also found a difference in allopreening depending on the outcome of a conflict occurring many hours earlier. From a functional perspective, allopreening may strengthen social bonds and group cohesion [41] or may be traded in return for some other commodity [42, 43], such as increased involvement in any future conflict.

Green woodhoopoe roosts are crucial for both survival and reproduction [10, 13]. If intergroup conflict affects the use of such limiting resources, as suggested by our work here, then there are likely implications for individual fitness beyond the obvious consequences of injury or death resulting from aggressive interactions themselves [16, 18]. Moreover, the increasing evidence that intergroup interactions affect intragroup behavior in a variety of species [7, 20, 37], not only

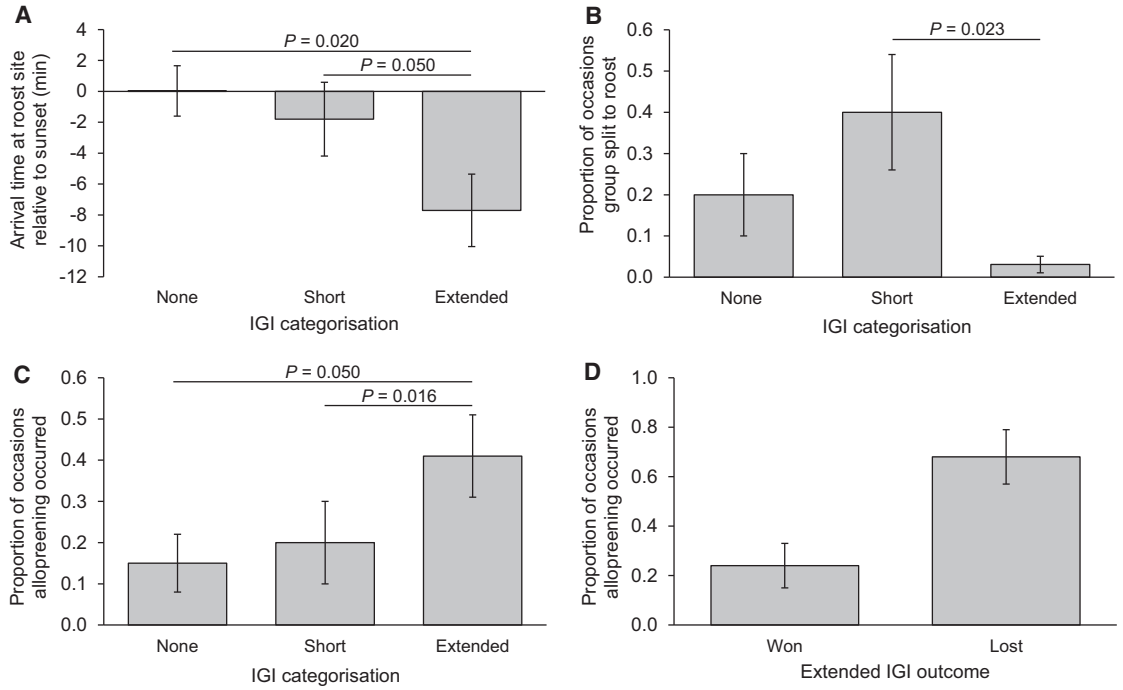

Figure 4. The Influence of Intergroup Interactions on Roost-Related Behavior

(A–C) The effect of IGI categorization (extended, short, or no IGI in the morning) on arrival time at the roost site that evening (A), the proportion of occasions in which the group split to roost between different sites (B), and the proportion of occasions in which group members allopreened at the roost site (C). (D) The effect of extended IGI outcome on the proportion of occasions in which allopreening occurred.
All panels show means ± SE, with p values for significant post hoc comparisons. n = 12 groups.

humans [6, 8, 21], suggests broad evolutionary significance. Although it has long been suggested that conflict with rival groups is a key selective driver for group dynamics and social structure [2, 5], previous empirical work on behavior has generally focused on immediate, short-term responses ([6, 7, 37], but see [9, 22]). The current study, showing that there can be a lasting impact of individual conflicts beyond the immediate effect of elevated stress, combined with the possibility that the mere threat of future conflicts also has an influence [16], suggests a stronger mechanism for evolutionary change. Future studies on intergroup conflict will therefore continue to be important in developing our understanding of resource use, sociality, and the evolution of cooperation.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.10.036.

Author Contributions

A.N.R. conceived the research and collected the data. T.W.F. conducted the statistical analyses. A.N.R. and T.W.F. interpreted the data and cowrote the paper.

Acknowledgments

This study complied with the laws of South Africa, where the data were collected, and was approved by the Science Faculty Animal Ethics Committee, University of Cape Town. We are grateful to Morné du Plessis for access to the study population he originally established and to Andrew Higginson, Christos Ioannou, and two anonymous referees for comments on the manuscript. The data were collected by A.N.R. while supported by a Natural Environment Research Council studentship.

Received: August 13, 2014
Revised: September 23, 2014
Accepted: October 13, 2014
Published: November 13, 2014

References

1. Radford, A.N. (2003). Territorial vocal rallying in the green woodhoopoe: influence of rival group size and composition. Anim. Behav. *66*, 1035–1044.
2. Bowles, S. (2009). Did warfare among ancestral hunter-gatherers affect the evolution of human social behaviors? Science *324*, 1293–1298.
3. Crofoot, M.C., and Wrangham, R.W. (2010). Intergroup aggression in primates and humans: the case for a unified theory. In Mind the Gap: Tracing the Origins of Human Universals, P.M. Kappeler and J. Silk, eds. (New York: Springer), pp. 171–195.
4. Hardy, I.C.W., and Briffa, M. (2013). Animal Contests (Cambridge: Cambridge University Press).
5. Van Schaik, C.P. (1989). The ecology of social relationships amongst female primates. In Comparative Socioecology: The Behavioural Ecology of Humans and Other Mammals, V. Standen and R. Foley, eds. (Oxford: Blackwell Scientific), pp. 195–218.
6. West, S.A., Gardner, A., Shuker, D.M., Reynolds, T., Burton-Chellow, M., Sykes, E.M., Guinnee, M.A., and Griffin, A.S. (2006). Cooperation and the scale of competition in humans. Curr. Biol. *16*, 1103–1106.
7. Radford, A.N. (2008). Duration and outcome of intergroup conflict influences intragroup affiliative behaviour. Proc. Biol. Sci. *275*, 2787–2791.
8. Puurtinen, M., and Mappes, T. (2009). Between-group competition and human cooperation. Proc. Biol. Sci. *276*, 355–360.
9. Crofoot, M.C. (2013). The cost of defeat: Capuchin groups travel further, faster and later after losing conflicts with neighbors. Am. J. Phys. Anthropol. *152*, 79–85.
10. Hawn, A.T., Radford, A.N., and du Plessis, M.A. (2007). Delayed breeding affects lifetime reproductive success differently in male and female green woodhoopoes. Curr. Biol. *17*, 844–849.

11. Radford, A.N., and du Plessis, M.A. (2004). Green woodhoopoe territories remain stable despite group-size fluctuations. J. Avian Biol. *35*, 262–268.
12. Radford, A.N., and du Plessis, M.A. (2003). Bill dimorphism and foraging niche partitioning in the green woodhoopoe. J. Anim. Ecol. *72*, 258–269.
13. Williams, J.B., du Plessis, M.A., and Siegfried, W.R. (1991). Green woodhoopoes (*Phoeniculus purpureus*) and obligate cavity roosting provide a test of the thermoregulatory insufficiency hypothesis. Auk *108*, 285–293.
14. du Plessis, M.A. (1992). Obligate cavity roosting as a constraint on dispersal of green (red-billed) woodhoopoes: consequences for philopatry and the likelihood of inbreeding. Oecologia *90*, 205–211.
15. Radford, A.N., and du Plessis, M.A. (2004). Territorial vocal rallying in the green woodhoopoe: factors affecting contest length and outcome. Anim. Behav. *68*, 803–810.
16. Radford, A.N. (2011). Preparing for battle? Potential intergroup conflict promotes current intragroup affiliation. Biol. Lett. *7*, 26–29.
17. Radford, A.N. (2012). Post-allogrooming reductions in self-directed behaviour are affected by role and status in the green woodhoopoe. Biol. Lett. *8*, 24–27.
18. du Plessis, M.A. (1993). Do group-territorial green woodhoopoes choose roosting partners on the basis of relatedness? Anim. Behav. *4*, 612–615.
19. Radford, A.N., and du Plessis, M.A. (2006). Dual function of allopreening in the cooperatively breeding green woodhoopoe, *Phoeniculus purpureus*. Behav. Ecol. Sociobiol. *61*, 221–230.
20. Radford, A.N. (2008). Type of threat influences postconflict allopreening in a social bird. Curr. Biol. *18*, R114–R115.
21. Erev, I., Bornstein, G., and Galili, R. (1993). Constructive intergroup competition as a solution to the free rider problem: a field experiment. J. Exp. Soc. Psychol. *29*, 463–478.
22. Markham, A.C., Alberts, S.C., and Altmann, J. (2012). Intergroup conflict: Ecological predictors of winning and consequences of defeat in a wild primate population. Anim. Behav. *82*, 399–403.
23. Harris, T.R. (2006). Between-group contest competition for food in a highly folivorous population of black and white colobus monkeys (*Colobus guereza*). Behav. Ecol. Sociobiol. *61*, 317–329.
24. Hsu, Y., Earley, R.L., and Wolf, L.L. (2006). Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes. Biol. Rev. Camb. Philos. Soc. *81*, 33–74.
25. Stamps, J.A., and Krishnan, V.V. (1997). Functions of fights in territory establishment. Am. Nat. *150*, 393–405.
26. Stamps, J.A., and Krishnan, V.V. (1998). Territory acquisition in lizards. IV. Obtaining high status and exclusive home ranges. Anim. Behav. *55*, 461–472.
27. Pride, R.E., Felantsoa, D., Randriamboavonjy, R., and Randriambelona, R. (2006). Resource defense in *Lemur catta*: the importance of group size. In Ringtailed Lemur Biology: *Lemur catta* in Madagascar, A. Jolly, R.W. Sussman, N. Koyama, and H. Rasamimanana, eds. (New York: Springer), pp. 208–232.
28. Mitani, J.C., Watts, D.P., and Amsler, S.J. (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. Curr. Biol. *20*, R507–R508.
29. Ligon, J.D., and Ligon, S.H. (199). Green woodhoopoes: life-history traits and sociality. In Cooperative Breeding in Birds, P.B. Slater and W.C. Koenig, eds. (Cambridge: Cambridge University Press), pp. 33–65.
30. Radford, A.N., and du Plessis, M.A. (2003). The importance of rainfall to a cavity nesting species. Ibis *145*, 692–694.
31. Christie, P., Oppliger, A., and Richner, H. (1994). Ectoparasite affects choice and use of roost sites in the great tit, *Parus major*. Anim. Behav. *47*, 895–898.
32. Fleischmann, D., Baumgartner, I.O., Erasmy, M., Gries, N., Melber, M., Leinert, V., Parchem, M., Reuter, M., Schaer, P., Stauffer, S., et al. (2013). Female Bechstein's bats adjust their group decisions about communal roosts to the level of conflict of interests. Curr. Biol. *23*, 1658–1662.
33. Conradt, L. (2012). Models in animal collective decision-making: information uncertainty and conflicting preferences. Interface Focus *2*, 226–240.
34. Kerth, G., Ebert, C., and Schmidtke, C. (2006). Group decision making in fission-fusion societies: evidence from two-field experiments in Bechstein's bats. Proc. Biol. Sci. *273*, 2785–2790.
35. Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., Connor, R., Di Fiore, A., Dunbar, R.I.M., Henzi, S.P., et al. (2008). Fission-fusion dynamics: new research frameworks. Curr. Anthropol. *49*, 627–654.
36. Sueur, C., King, A.J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C., Schaffner, C.M., Williams, L., Zinner, D., and Aureli, F. (2011). Collective decision-making and fission–fusion dynamics: a conceptual framework. Oikos *120*, 1608–1617.
37. Polizzi di Sorrentino, E., Schino, G., Massaro, L., Visalberghi, E., and Aureli, F. (2012). Between-group hostility affects within-group interactions in tufted capuchin monkeys. Anim. Behav. *83*, 445–451.
38. Schino, G., Scucchi, S., Maestripieri, D., and Turilazi, P.G. (1988). Allogrooming as a tension-reduction mechanism: a behavioural approach. Am. J. Primatol. *16*, 43–50.
39. Aureli, F., Preston, S.D., and de Waal, F.B.M. (1999). Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): a pilot study. J. Comp. Psychol. *113*, 59–65.
40. Aureli, F., and Yates, K. (2010). Distress prevention by grooming others in crested black macaques. Biol. Lett. *6*, 27–29.
41. Dunbar, R.I.M. (1991). Functional significance of social grooming in primates. Folia Primatol. (Basel) *57*, 121–131.
42. Seyfarth, R.M., and Cheney, D.L. (1984). Grooming, alliances and reciprocal altruism in vervet monkeys. Nature *308*, 541–543.
43. de Waal, F.B.M. (1997). The chimpanzee's service economy: food for grooming. Evol. Hum. Behav. *18*, 375–386.